

Discovery of *Dichocrocis frenatalis* Lederer, 1863 (Lepidoptera, Crambidae, Spilomelinae) in mangrove environments of the Ryukyu Islands, Japan, and tribal placement of the genus

Yuki Matsui¹, Nakatada Wachi², Yutaka Yoshiyasu³

¹ Entomological Laboratory, Faculty of Agriculture, Kyushu University, 744 Motoooka, Nishi-ku, Fukuoka 819-0395, Japan

² Iriomote Station, Tropical Biosphere Research Center, University of the Ryukyus, 870 Uehara, Taketomi, Yaeyama, Okinawa 907-1541, Japan

³ Laboratory of Applied Entomology, Graduate School of Life and Environmental Science, Kyoto Prefectural University, Shimogamo, Kyoto 606-8522, Japan

Corresponding author: Yuki Matsui (mothya22@gmail.com)

Abstract

Dichocrocis frenatalis Lederer, 1863, the little-known type species of the polyphyletic genus *Dichocrocis*, was discovered in the Ryukyu Islands, Japan. We provide a redescription of the adult morphology, including the male genitalia with highly developed hair-pencil structures, as well as female genitalia. The phylogenetic placement of this genus, and therefore its type species, within Spilomelinae has been uncertain, but our molecular phylogenetic analysis and morphological evaluation support the placement of the genus *Dichocrocis* in the tribe Steniini. Additionally, as a novel ecological observation, we report that the Japanese population of this species is abundant in mangrove environments, where the adults frequently aggregate on the underside of leaves and are preyed upon by a mangrove-associated robber fly.

Key words: Adults aggregation, hair-pencils, polyphyletic genus, Steniini, type species



Academic editor: Richard Mally

Received: 15 April 2025

Accepted: 14 May 2025

Published: 25 June 2025

ZooBank: <https://zoobank.org/0EE119E1-5114-46F9-B265-B2F09321409B>

Citation: Matsui Y, Wachi N, Yoshiyasu Y (2025) Discovery of *Dichocrocis frenatalis* Lederer, 1863 (Lepidoptera, Crambidae, Spilomelinae) in mangrove environments of the Ryukyu Islands, Japan, and tribal placement of the genus. ZooKeys 1243: 143–158. <https://doi.org/10.3897/zookeys.1243.155924>

Copyright: © Yuki Matsui et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

The genus *Dichocrocis* Lederer, 1863 was established by monotypy for *D. frenatalis* Lederer, 1863 from the Nicobar Islands, India. Hampson (1896) synonymized the type species with *Botys pandamalis* Walker, 1859 and expanded the genus definition based on unreliable external morphological evidence such as the shape of palpi and legs, and wing venation. Although Hampson's classification was heterogeneous, as it included species belonging to *Conogethes*, *Gadessa*, *Orthospila*, and *Rehimena*, each of which is now recognized as valid genera, it was nevertheless followed by many subsequent authors (e.g., Pajni and Rose 1977; Mandal and Bhattacharya 1979). Among these genera, the separation of *Conogethes* from *Dichocrocis* became widely accepted after the 1980s (e.g., Inoue 1982; Inoue and Yamanaka 2006), but no formal explanation was provided for this treatment. Recently, Mally et al. (2019) transferred *D. pandamalis* to *Conogethes* based on morphological and molecular evidence. Currently, *D. frenatalis*, the genus type species, is regarded as a valid species, and the genus *Dichocrocis* comprises 53 described species mainly from the

Paleotropics (Nuss et al. 2025). However, the original description of the type species provides only a brief account of its external morphology, and no detailed morphological study has been conducted on this species to date. As a result, the taxonomic definition and diagnostic characters of the genus remain ambiguous. Although Mally et al. (2019) examined the male genitalia of *D. frenatalis* (from Sumatra, Indonesia) and suggested its tribal placement in Steniini, they did not formally assign the genus to that tribe.

No *Dichocrocis* species had previously been recorded in Japan. Recently, however, we discovered *D. frenatalis* on Okinawa, Ishigaki, and Iriomote Islands, in the Ryukyu Islands of southwestern Japan. In this study, we redescribe *D. frenatalis* and assign *Dichocrocis* to a spilomeline tribe based on morphological investigations and molecular phylogenetic analysis. We also report for the first time the occurrence of this species in a mangrove environment on Iriomote Island, where the adults frequently aggregate on the underside of leaves and are preyed upon by a mangrove-associated robber fly.

Materials and methods

Most *Dichocrocis frenatalis* specimens were collected by daytime search in a mangrove environment on Iriomote Island (Funaura), with some additional specimens obtained through light trapping at various localities on Okinawa, Ishigaki, and Iriomote Islands. The specimens were deposited in the Entomological Laboratory of Kyushu University, Japan (**ELKU**); the Laboratory of Environmental Zoology and Entomology, Osaka Metropolitan University, Japan (**OMU**); the Ryukyu University Museum (Fujukan), Japan (**RUMF**); or the Iriomote Station, Tropical Biosphere Research Center, University of the Ryukyus, Japan (**TBRC**). The specimens preserved at the National Museum of Nature and Science, Japan (**NSMT**) were also examined. Methods for morphological observation and genitalia dissection are described in Matsui et al. (2024). Morphological terminology follows Maes (1985) for tympanal organs, Downey and Allyn (1975) for hair-pencil scales, and Mally et al. (2019) for all other structures. Forewing lengths of males and females were compared using Welch's two-sample *t*-test in R v. 4.4.2 implemented in WebR (<https://github.com/r-wasm/webr>). Mean and standard deviation (SD) of the forewing lengths were also calculated for each sex.

One specimen of *D. frenatalis* (♂, Funaura, Iriomote Island, 14 July 2023, NW leg.) was used for DNA analysis. The methods for DNA extraction, PCR reaction, and sequencing follow Matsui et al. (2022, 2024). Briefly, the entire COI gene and fragments of genes RpS5, CAD, and EF1α were sequenced using primer sets described in Matsui et al. (2022). The obtained sequences were aligned and manually corrected using MEGA v. 7.0 (Kumar et al. 2016) with the dataset of the same regions by Matsui et al. (2022). A maximum-likelihood tree was constructed using IQ-TREE v. 2.3.1 (Minh et al. 2020). The concatenated dataset was partitioned by gene and codon position, and the best-fitting nucleotide substitution models were selected using ModelFinder implemented in IQ-TREE based on the Bayesian information criterion (BIC). Branch supports were calculated using Ultrafast Bootstrap (UFBT) and Shimodaira-Hasegawa-like approximate likelihood ratio tests (SH-aLRT) implemented in IQ-TREE each with 1,000 replicates. The obtained sequences were deposited in DDBJ (<https://www.ddbj.nig.ac.jp/>) (accession numbers: COI: LC867066, RpS5: LC867065, CAD: LC867063, and EF1α: LC867064).

English editing was supported by OpenAI's ChatGPT (GPT-4) under the supervision of the authors.

Results

Taxonomy

Dichocrocis frenatalis Lederer, 1863

Figs 1–7

(Japanese name: nettai-kurosuji-ki-nomeiga)

Dichocrocis frenatalis Lederer, 1863: 448, pl. 17 fig. 15; Moore 1877: 616; Mally et al. 2019: electronic supplement file 1; Rao and Sivaperuman 2020: 20; Whitaker et al. 2023: 54.

Dichocrocis pandamalis (part): Hampson 1896: 306.

Diagnosis. This species is externally similar to *Conogethes pandamalis* but can be distinguished by the continuous postmedial line straight from costa to CuA₂ in the forewing (in *C. pandamalis* it is interrupted and protruded between M₂ and CuA₂), and the narrow and black terminal line in both wings (in *C. pandamalis* the terminal line is lacking). Several undescribed species that are possibly congeneric have been found in Borneo [cf. *Dichocrocis* sp. 1–9 of Whitaker et al. (2023)] and on the Andaman Islands (B. Sumit Kumar Rao pers. comm.), but *D. frenatalis* can be distinguished from these species based on the aforementioned characters. *Dichocrocis* sp. 15 and 16 of Whitaker et al. (2023) most resemble *D. frenatalis*, but they are best distinguished by broad terminal lines on both wings (in *D. frenatalis* they are very narrow).

Redescription. Head (Fig. 1A). Frons yellowish orange, smooth. Vertex with yellow scales, anterior scales porrect, posterior scales erect. Maxillary palpus pale yellow, minute. Labial palpus yellow, upturned, first and second palpomeres with raised scales ventrally. Ocellus distinct, brownish, touching compound eye. Chaetosemata absent. Antennae about 4/5 of forewing length, light brown, dorsally covered with pale yellow scales, ciliate in male, filiform in female; scape yellow. Proboscis covered with yellow scales basally.

Thorax and legs. Thorax yellowish orange dorsally, pale yellow ventrally. Legs almost pale yellow; foreleg tibia with a bold blackish brown band medially; midleg tibia with a pair of spurs, inner spur about 2/3 length of outer one; hindleg tibia with two pairs of spurs, respective inner spurs about 2 times longer than outer ones.

Wings (Fig. 1B–D). Forewing length 6.00–8.80 mm (Suppl. material 1: table S1). The mean forewing length (\pm SD) was 7.10 ± 0.85 mm for males ($n = 10$) and 7.09 ± 0.71 mm for females ($n = 10$), with no statistically significant difference between sexes ($t = -0.029$, $df = 17.387$, $p = 0.978$). Forewing ground color yellowish orange; basal fleck black, ending around Cu vein; antemedial line black, gently excurved; postmedial line black, straight from costa to CuA₂ vein, incurved at a right angle on CuA₂ vein, then oblique toward dorsum; marginal line black and narrow, running along termen; discocellular lunule black, nearly V-shaped; cell with a small black dot inside the discocellular lunule, but often disappearing; cilia pale yellow, banded with brownish orange medially. Hindwing ground color yellowish orange; discocellular lunule a black bar, often

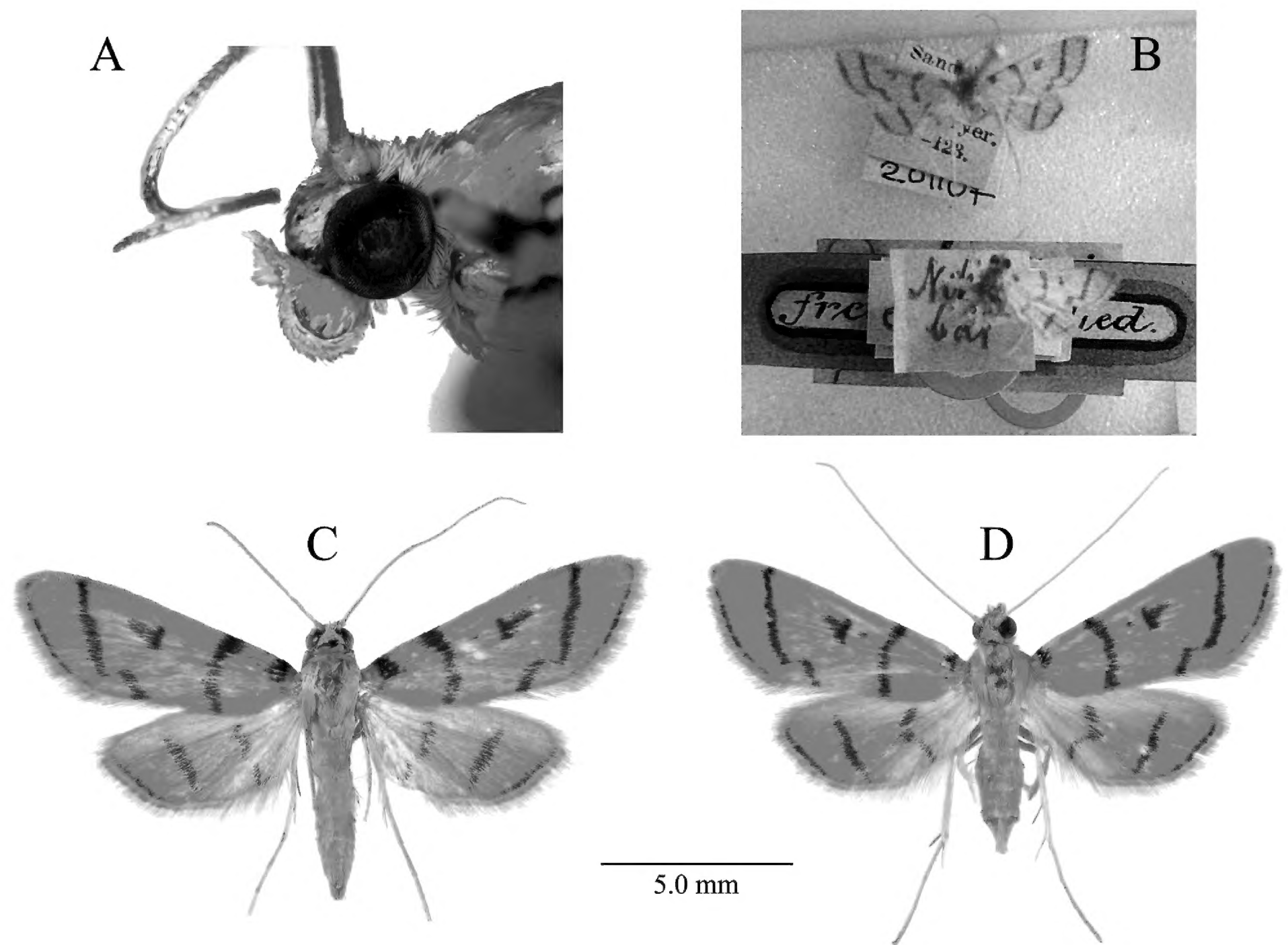


Figure 1. *Dichocrocis frenatalis* adults. **A.** Head; **B.** The holotype (bottom) preserved in NHMUK (photo by Richard Mally); **C.** Male; **D.** Female.

connected with postmedial line; postmedial line black, straight from costa to distal CuP vein, strongly narrowed (often disappearing there) and incurved at an acute angle between veins CuA₂ and CuP veins, running toward discocellular lunule, then thicken again and extending to dorsum; marginal line as in that of forewing, disappearing around tornus; cilia concolorous with that of forewing. In males, both wings tend to be narrower and each line thicker than in the female. Both wings underneath pale yellowish orange with the same maculation as above, but slightly weaker.

Wing venation (Fig. 2). Forewing Sc and R₁ separate; R₂ concurrent with R₃+R₄ basally; R₃ stalked with R₄ at 1/4 distance from cell; R₅, M₁, M₂, M₃, CuA₁, and CuA₂ separate, almost equidistant; A₁₊₂ weakly sinuate near tornus; A₃ weak, straight; discal cell closed; male retinacular hook absent. Hind wing Sc+R₁ stalked with Rs at 4/5 of length; M₁ stalked with Sc+R₁ at upper angle of cell; M₂, M₃, and CuA₁ close basally; CuA₂ distant from CuA₁; CuP and A₁₊₂ strong; A₃ strong, weakly sinuate; female with two frenular bristles.

Abdomen. Yellowish orange; in male, terminal segment enlarged, hair-pencils often visible (Fig. 3A). Tympanal organs (Fig. 3B, C) with praecinctorium not bilobed; tympanum and conjunctivum forming a shallow angle medially; bulla tympani relatively small and narrow, anterior margin truncate; fornix tympani protruded ventrally; saccus tympani extending about 1/3 of 2nd sternite, with straight posterior ridge; venula secundae absent. Male 8th tergite (Fig. 3C) with

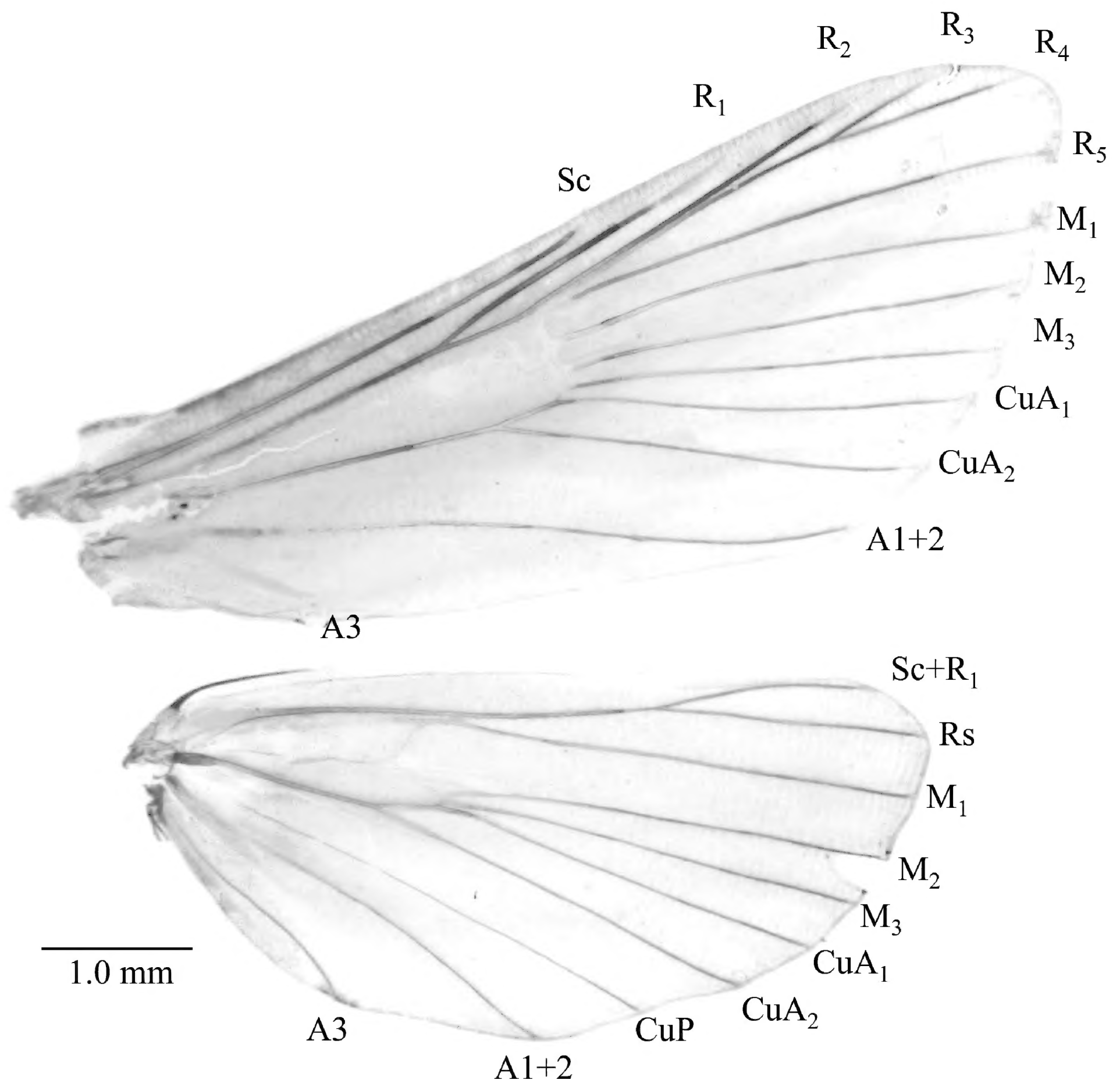


Figure 2. *Dichocrocis frenatalis* female wing venation.

a broad longitudinal sclerotization, its anterior end Y-shape, lateral margins tapered posteriorly, posterior end with strong wrinkles; both sides of posterior portion with a short linear sclerotization. Male 8th sternite with two longitudinal sclerotizations, connected to strongly sclerotized and anteriorly convex anterior margin (Fig. 3C).

Male genitalia (Figs 4, 5). Tuba analis (ta) weakly sclerotized, about 2.5 times longer than uncus. Uncus narrow, curved ventrad, apex covered with ventrally directed and bifid chaetae. Tegumen somewhat broad, tapered toward uncus. Parateguminal sclerite [*sensu* Solis et al. (2020)] extending from tegumen complicated in structure, composed of a saddle-shaped pad (sp) dorsally and a larger triangular sclerite (ts) ventrally, each with hair-pencils consisting of six types of specialized scales: the entire sclerite with many tufts of slender spatulate scales (ss), the dorsal and ventral tufts strongly bent inwardly, otherwise bent in various directions; the saddle-shaped pad dorsally with a tuft of somewhat broad

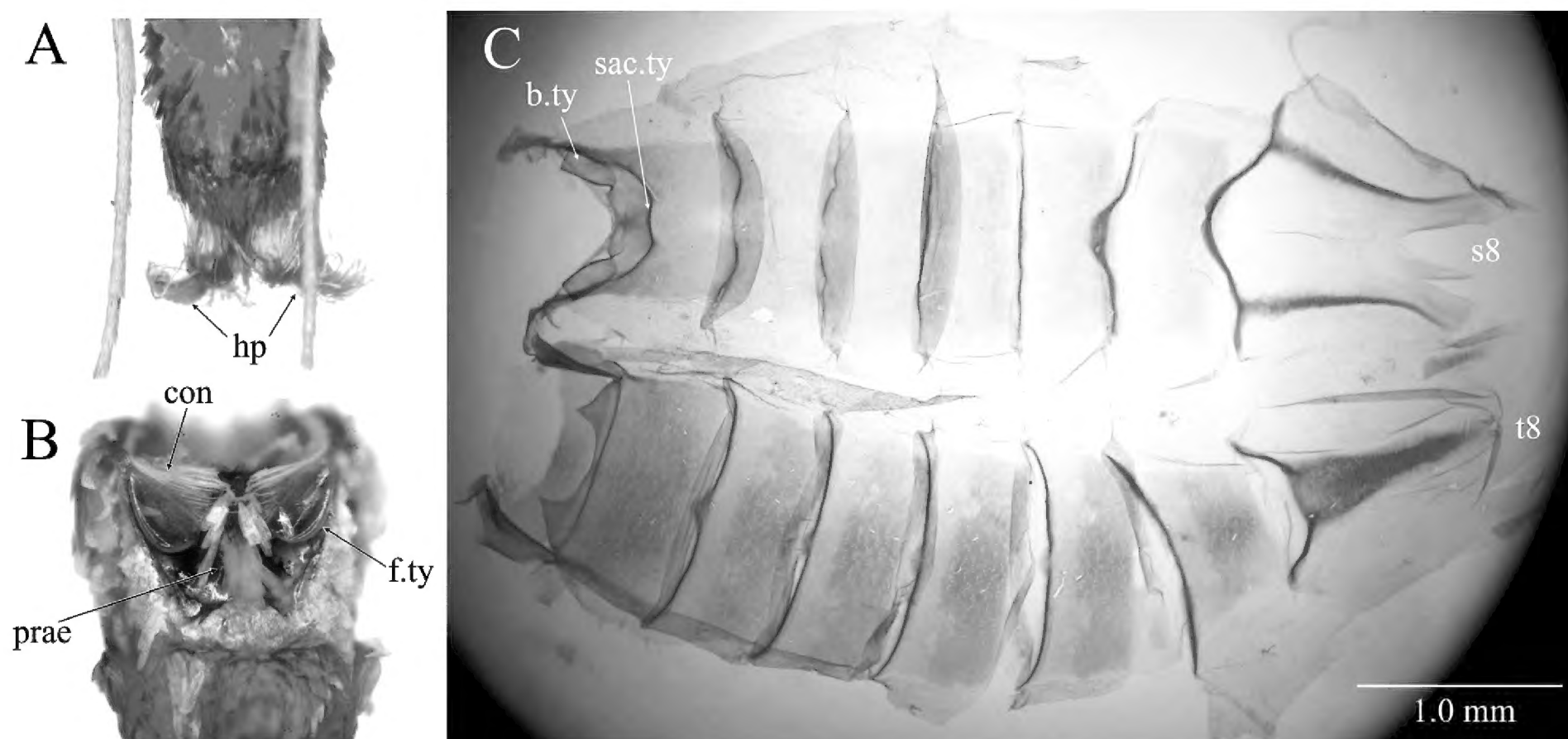


Figure 3. *Dichocrocis frenatalis* abdominal structures. **A.** Male abdominal tip with visible hair-pencils (indicated by arrows); **B.** Tympanal organs; **C.** Male abdominal cuticle (slide no. YM878). b.ty: bulla tympani, con: conjunctivum, f.ty: fornix tympani, hp: hair-pencils, prae: praecinctorium, sac.ty: saccus tympani, s8: sternite 8, t8: tergite 8.

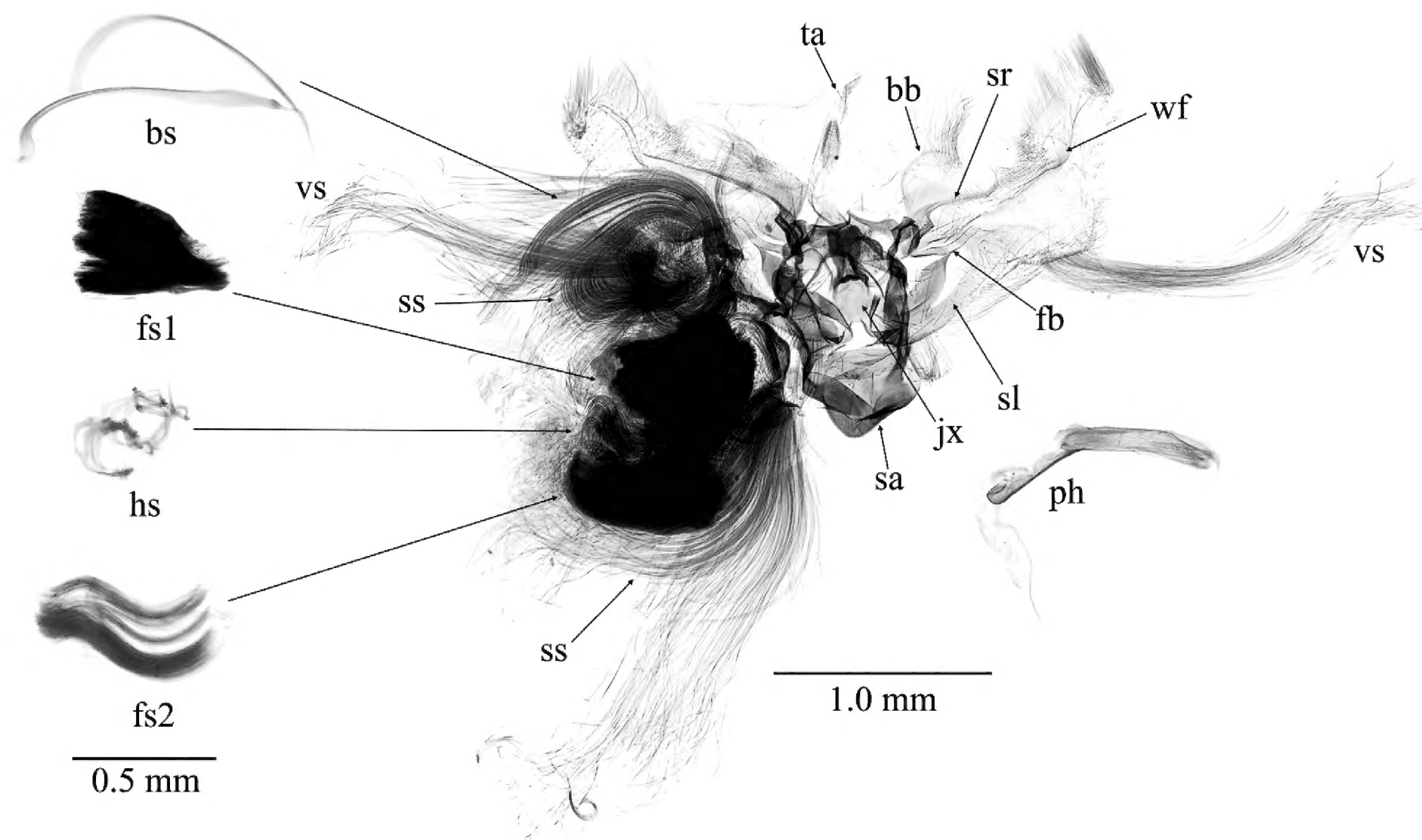


Figure 4. *Dichocrocis frenatalis* male genitalia (slide no. YM878). bb: basal bulge of valva costa, bs: broad spatulate scale, fb: fibula, fs1: filiform scale 1, fs2: filiform scale 2, hs: hook-shaped scale, jx: juxta, ph: phallus, sa: saccus, sl: sacculus, sr: sclerotized ridge of valva costa; ss: slender spatulate scale, ta: tuba analis, vs: valva setae, wf: wavy furrow.

spatulate scales (bs) that ventrally bent and distally tapered; the triangular sclerite with a tuft of long, lamellate scales (ls) at its apex, and a cluster consisting of short, blackish brown filiform scales (fs1), longer and brown filiform scales (fs2), and short hook-shaped scales (hs) internally. Gnathos absent. Saccus (sa) large and broad in dorsoventral view, rounded. Valva costa with a straight sclerotized

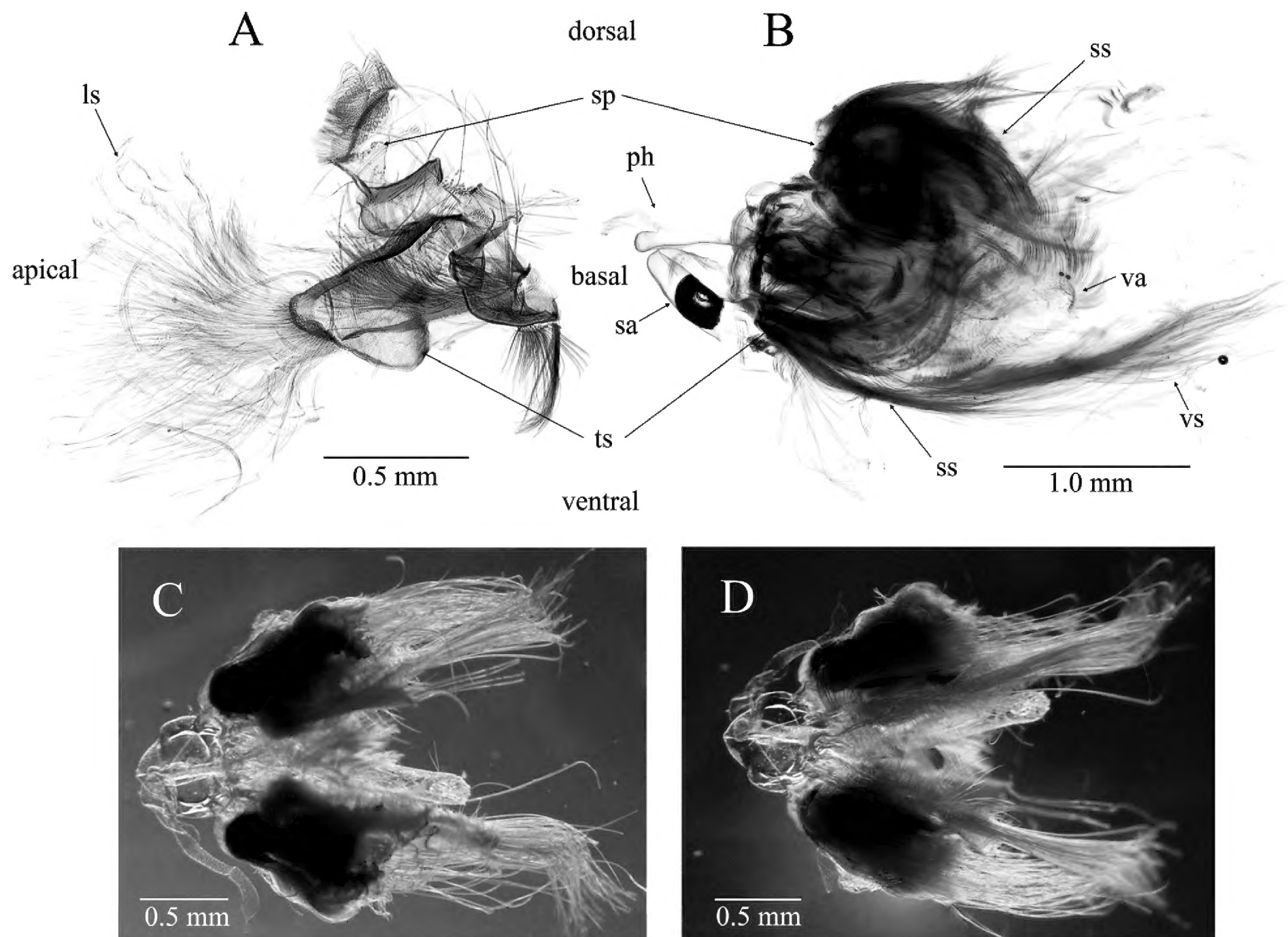


Figure 5. *Dichocrocis frenatalis* male genitalia. **A.** Parateguminal sclerites (most scales removed, slide no. YM1276); **B.** Whole genitalia, unmounted, left lateral view (internal hair-pencil scales removed); **C.** Whole genitalia, unmounted, dorsal view; **D.** Ditto, dorsal view; **D.** Ditto, ventral view. ls: lamellate scale 1, ph: phallus, sa: saccus, sp: saddle-shaped pad, ts: triangular sclerite, ss: slender spatulate scale, vs: valva setae.

ridge (sr) extending distal 1/4 and a large rounded basal bulge (bb), costal margin strongly concave at the termination of the ridge, dorsally with dense hair-like setae; inner surface with a wavy furrow (wf) running from apex to basal 2/3; ventral margin subtriangularly bulged medially, its apex with a tuft of long hair-like setae (vs); fibula (fb) spatula-shaped, basally separates into two arms, ventral arm concurrent with saccular base; sacculus (sl) a membranous band. Transtilla narrow, weakly connected medially. Juxta (jx) elongate, medially constricted with two longitudinal ridges, dorsal margin truncate, ventral margin medially concave and laterally connected to basal sacculus. Phallus (ph) with antero-ventrally extended caecum; vesica covered with fine microspines, without cornuti.

Female genitalia (Fig. 6). Papillae anales broad. Anterior apophyses slightly curved, apex blunt. Posterior apophyses broader than anterior ones, dilated near base. Antrum somewhat narrow, membranous, funnel-shaped. Ductus bursae membranous, sclerotized near corpus bursae, lateral margins of the sclerotization lightly tapered (Fig. 6C). Ductus seminalis emerging from the posterior end of ductus bursae. Spermathecal gland with lagena. Corpus bursae ellipsoid, 1/5 from anterior end with a transverse band composed of needle-like spines (ca 0.15–0.30 mm, Fig. 6D), and anterior portion from it sparsely covered with similar but shorter spines (ca 0.07–0.09 mm, Fig. 6D).

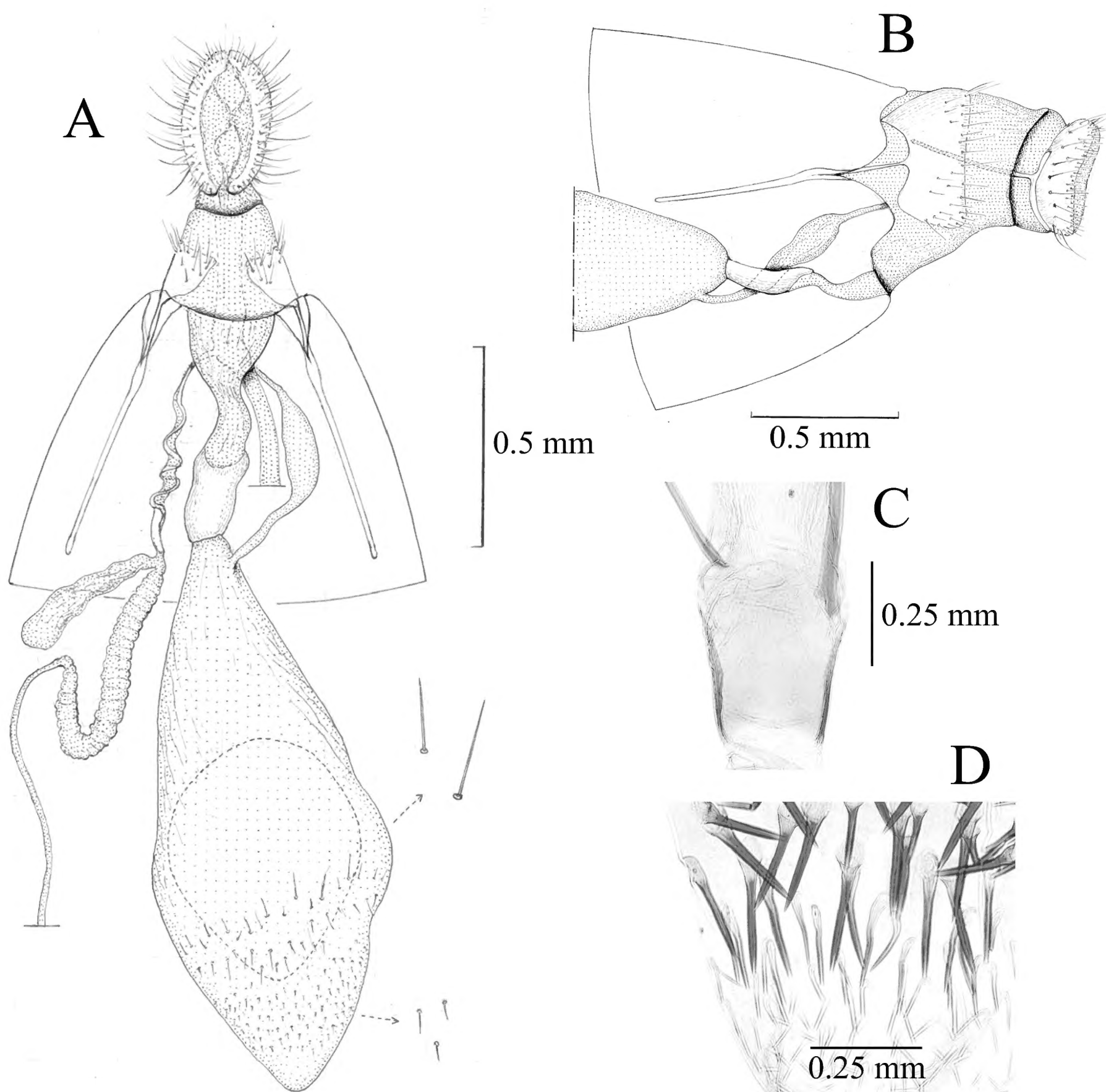


Figure 6. *Dichocrocis frenatalis* female genitalia. **A.** Whole genitalia, ventral view, spermatophore in the corpus bursae indicated by dotted circle (illustration by YY); **B.** 8th to 10th abdominal segments, lateral view (spermathecal gland excluded); **C.** Sclerotization of ductus bursae, magnified view (slide no. YM877); **D.** Spines on corpus bursae, magnified view (slide no. YM877).

Material examined (n = 212 individuals). **Okinawa I.** • 2♂; Nago-shi, Ôura; 1 July 2009; U. Jinbo; NSMT. **Ishigaki I.** • 1♀; Takeda-rindô; 21 May 2009; U. Jinbo; NSMT; • 1♂; Yarabe-rindô; 22 Aug. 2022; I. Aoki; gen. slide no. YM878; ELKU. **Iriomote I.** • 1♀; Tedô-san parking; 30 May 2015; Y. Matsui; LT; ELKU; • 1ex.; ditto; 5 Apr. 2024; T. Mano; LT; ELKU; • 1♂; Sonai; 11 Jan. 2023; Y. Yoshiyasu; OMU; • 1♂1♀; ditto; 4 June 2024; T. Mano; • 2♀; Haemi; 22 to 24 Nov. 2019; F. Ishiwata; gen. slide no. YM876, 877; ELKU; • 3♀; ditto; 6 Oct. 2024; T. Mano; • 4♂5♀; Komi; 25 May 2009; U. Jinbo; NSMT; • 1♂; Funaura; 22 Sep. 2000; M. Kinjo & S. Katada; RUMF; • 1♀; ditto; 4 Oct. 2000; M. Kinjo & S. Katada; RUMF; • 1♂; ditto; 18 Jan. 2001; M. Kinjo & S. Katada; RUMF; • 1♀; ditto; 25 May 2009; U. Jinbo; NSMT; • 3♂2♀; ditto; 4 Apr. 2023; N. Wachi; TBRC and ELKU; • 5♂3♀; ditto; 21 Apr. 2023; N. Wachi; TBRC and ELKU; • 2♂; ditto; 24 Apr. 2023; N. Wachi; TBRC; •

4♀; ditto; 2 May 2023; N. Wachi; TBRC; • 3♀; ditto; 5 May 2023; N. Wachi; TBRC; • 5♂2♀; ditto; 20 May 2023; N. Wachi; TBRC; • 7♂1♀; ditto; 23 May 2023; N. Wachi; TBRC and ELKU; • 4♂1♀; ditto; 3 June 2023; N. Wachi; TBRC; • 5♂2♀; ditto; 6 June 2023; N. Wachi; TBRC and ELKU; • 4♀; ditto; 26 June 2023; N. Wachi; TBRC; • 4♂6♀; ditto; 4 July 2023; N. Wachi; TBRC; • 2♂2♀; ditto; 7 July 2023; N. Wachi; TBRC; • 2♂4♀; ditto; 12 July 2023; N. Wachi; TBRC; • 4♂4♀; ditto; 14 July 2023; N. Wachi; TBRC; • 1♂1♀; ditto; 13 Mar 2024; N. Wachi; TBRC; • 1 ex.; ditto; 4 Jun 2024; N. Wachi; prey of *Maira aenea* (Fabricius) (Diptera: Asilidae); iNaturalist observation ID: 220722951; TBRC; • 1 ex.; ditto; 18 Jun 2024; N. Wachi; prey of *M. aenea*; iNaturalist observation ID: 224300521; TBRC; • 2 ♂; ditto; 26 Mar 2025; N. Wachi; TBRC; • 4♂3♀; ditto; 9 Apr 2025; N. Wachi; TBRC; • 1 ♀; ditto; 3 Dec. 2024; Y. Matsui & N. Wachi; ELKU; • other 90 individuals; ditto; N. Wachi; TBRC (see Suppl. material 2: table S2).

Distribution. India (Nicobar Islands) (Lederer 1863), Indonesia (Sumatra Island) (Mally et al. 2019), Hong Kong (Whitaker et al. 2023), Japan (Okinawa, Ishigaki, and Iriomote Islands) (this study).

Biological notes. Our collection data suggest that the adults occur almost year-round. In the mangrove environment of Funaura, Iriomote Island, aggregations of adults on the underside of leaves were occasionally observed during the day (Fig. 7A, B). The aggregations included both sexes, although males were significantly more numerous. Some adults were observed being preyed upon by a robber fly, *Maira aenea* (Fabricius) (Diptera, Asilidae) (Fig. 7C, D). The occurrence of this robber fly in mangrove environments has been reported in previous studies (Utsugi 2006; Tomazovic and Grootaert 2010).

Tribal placement. The results from our molecular phylogenetic analysis placed *D. frenatalis* in Steniini (see below). In addition, the following genital characters, as proposed by Mally et al. (2019) for Steniini, support this placement: bifid uncus chaetae, undulated valva costa, well-separated valva fibula and distal sacculus, broad saccus, phallus with caecum, and corpus bursae with spinose texture and lacking signa. Since *D. frenatalis* is the type species of *Dichocrocis*, we assign the genus to the tribe Steniini.

Remarks. In this study, we identified the Japanese specimens of this species as *D. frenatalis* based on the wing maculation of the type specimen (abdomen missing) preserved in the Natural History Museum, London, UK (NHMUK) (Fig. 1B), in addition to the original description. We consider this identification to be justified at this time for the following reasons: 1) the abdomen of the type specimen is lost, rendering identification based on genitalia impossible, 2) no additional specimens of this species have been collected at the type locality (B. Sumit Kumar Rao pers. comm.), and 3) although Whitaker et al. (2023) illustrated many (putative) *Dichocrocis* species, none of them exhibit wing maculation matching that of *D. frenatalis*.

Molecular phylogenetic analysis

The entire COI gene, partial CAD, RpS5, and EF1α genes from the Japanese specimen of *D. frenatalis* were sequenced for the first time. No matching or closely related sequences were found in the BOLD (<https://boldsystems.org/>) or GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>) databases. *Dichocrocis frenatalis* is recovered within the strongly supported monophyletic Steniini

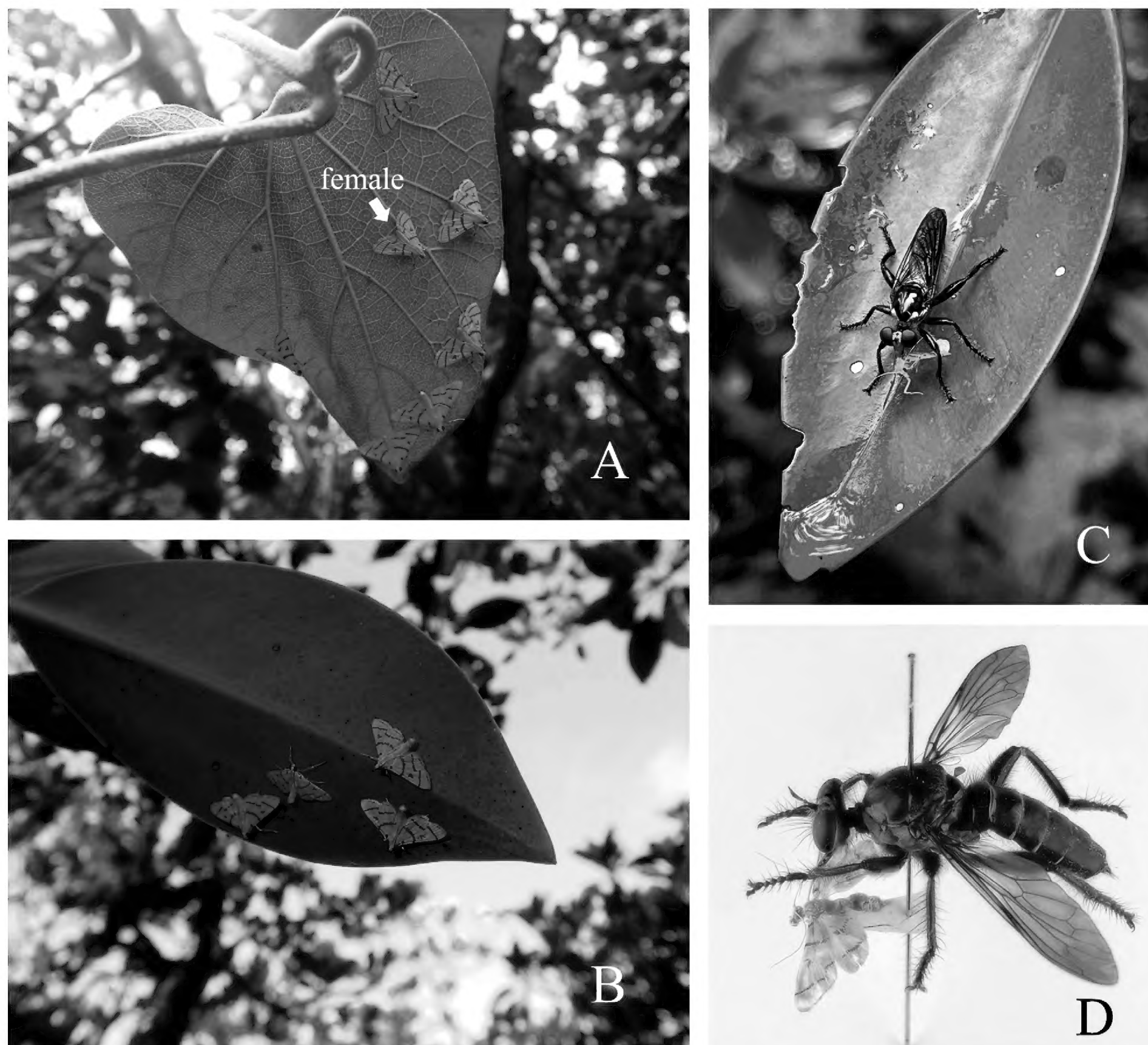


Figure 7. Biology of *Dichocrocis frenatalis* in Funaura, Iriomote Island, Japan. **A.** Aggregation of adults on the underside of a leaf (23 May 2023), a female is indicated by an arrow, while the others are males; **B.** Aggregation of male adults on the underside of a leaf (26 Aug. 2023); **C.** An adult preyed upon by a mangrove-associated robber fly, *Maira aenea* (Diptera: Asilidae) [18 June 2024, photo by Nakatada Wachi (@wachinakatada); <https://www.inaturalist.org/observations/224300521>; accessed on 11 Mar. 2025] **D.** Pinned specimens of the robber fly and its moth prey in Fig. 7C.

(SH-aLRT = 89.6, UFBT = 98) in the maximum likelihood tree (Fig. 8). Most relationships within Steniini are significantly supported (SH-aLRT \geq 80, UFBT \geq 95), and *D. frenatalis* is the sister taxon to a clade consisting of *Metasia* and paraphyletic *Nacoleia* [“group 1” *sensu* Matsui et al. (2022)] species with near-maximum support values (SH-aLRT = 99, UFBT = 100).

Discussion

In this study, we provide the first detailed redescription of *Dichocrocis frenatalis*, the type species of *Dichocrocis*. The genus is taxonomically problematic as a polyphyletic and speciose genus within Spilomelinae (Mally et al. 2019). This issue likely originates from Hampson’s (1896) taxonomic treatment, which syn-

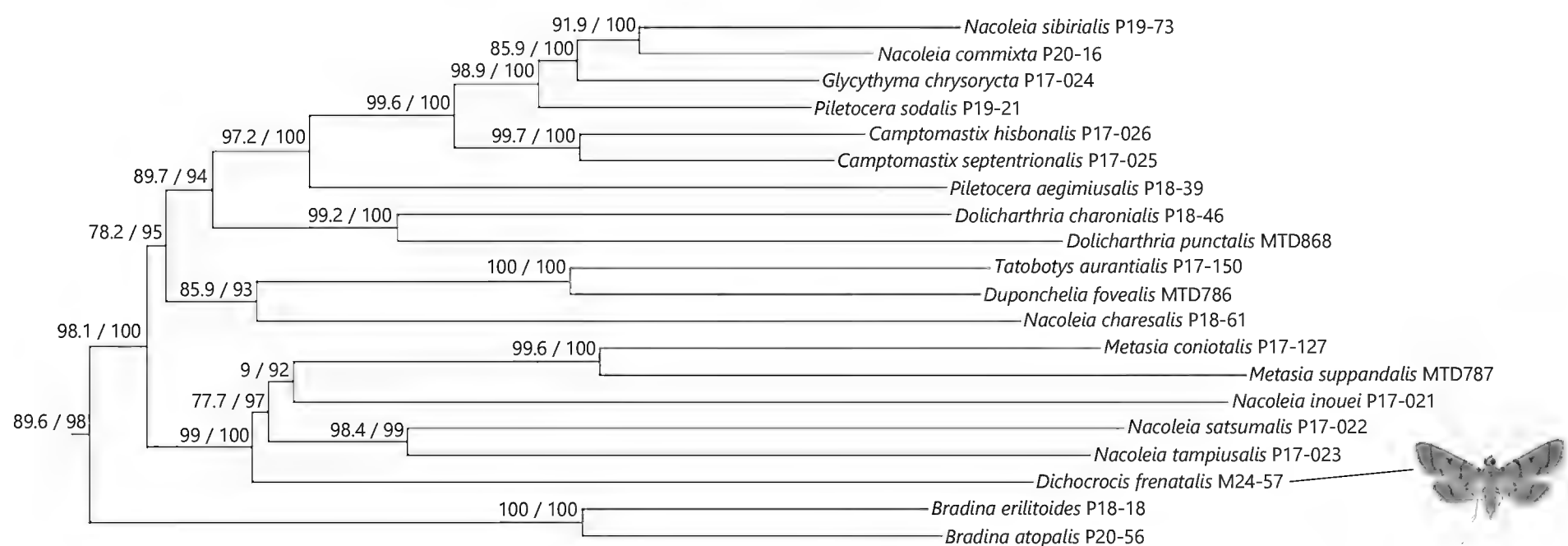


Figure 8. A maximum-likelihood (ML) phylogeny based on four-gene dataset (the parts other than the tribe Steniini are omitted). The numbers at each node indicate the Shimodaira-Hasegawa-like approximate likelihood ratio tests (SH-aL-RT) / ultrafirst bootstrap (UFBT).

onymized *D. frenatalis* with *C. pandamalis*. These two species belong to distant lineages: the former is in the Steniini, as shown in this study, while the latter belongs to the genus *Conogethes* in the tribe Margaroniini. Since *C. pandamalis*, erroneously regarded by Hampson (1896) as the type species of *Dichocrocis*, is a member of Margaroniini, several species of Margaroniini are still misplaced in *Dichocrocis*. For example, molecular and morphological analyses by Mally et al. (2019) confirmed that *D. zebralis* (Moore, 1867) belongs to the *Glyphodes* genus group sensu Sutrisno (2002) in Margaroniini. In addition, the male and female genitalia of *D. klotsi* Pajni & Rose, 1977, as described in the original description, suggest that its placement near or in *Conogethes*. The morphological information of the type species provided here should serve as a basis for re-assessing the placement of other members currently assigned to *Dichocrocis*.

The males of *D. frenatalis* have remarkably well-developed, complex hair-pencils compared to other Spilomelinae species. Similarly complicated hair-pencils are also found in *Camptomastix* and *Piletocera* species in the same tribe (Mally et al. 2019; YM pers. obs.). Generally, hair-pencils attached to male genitalia are believed to be associated with pheromone release and/or storage (Birch et al. 1990), although their function has been experimentally demonstrated in only a few studies, including Spilomelinae. One such example is *Conogethes punctiferalis*, in which the male has hair-pencils consisting of four types of scales, and washing these scales with an organic solvent or removing them significantly reduces their mating success (Kimura and Honda 1999; Kimura et al. 2002). Interestingly, the four types of male hair-pencil scales in *C. punctiferalis* exhibit functional differentiation: male pheromones are contained exclusively in the retiform and filiform scales, which are located inside the hair-pencil-complex and are easily detached, whereas the outer phylliform and spatulate scales appear to protect the inner scales (Kimura et al. 2002). The six types of scales found in *D. frenatalis* likely exhibit functional differentiation, similar to those in *C. punctiferalis*: the filiform scales are located inside the hair-pencil complex and are easily detached, while the other scales are relatively robust and cover the filiform scales. Further investigation using electron microscopy and chemical analyses will help elucidate the function of the hair-pencil scales in *D. frenatalis*.

Given that the adults of *D. frenatalis* were found in mangrove environments in this study, their life history is probably closely associated with mangroves, although the immature stages of this species remain unknown. Most species of Steniini are detritivorous as far as known (Mally et al. 2019; Matsui et al. 2022). However, while the detritivorous species in this tribe easily lay eggs on the walls of housed plastic containers, the tested females of *D. frenatalis* did not do so (YM pers. obs.), suggesting a different feeding habit. Two other members of Steniini, *Tatobotys janapalis* (Walker) and *T. aurantialis* Hampson are also abundant in mangrove habitats. The former feeds on mangrove flowers and buds (Murphy 1990), and the latter on red algae submerged in seawater (Yoshiyasu 2017). As with these species, *D. frenatalis* may depend on specific resources other than detrital matter in mangrove environments.

Daytime aggregations of adults on the underside of leaves have been reported in some hygrophilous crambid taxa, including *Eristena* and *Strepsinoma* (Acentropinae) (Yoshiyasu 1984; Robinson et al. 1994; Speidel and Mey 1999), as well as *Taurometopa* (Odontiinae) (Murphy 1990), but, to our knowledge, not in Spilomelinae. Murphy (1990) considered the assemblage of *T. pyrometalla* Meyrick as a “lek” because all members of the assemblage were males with sexually dimorphic (larger) heads. The observed assemblages of *D. frenatalis* include more males than females, but do not exhibit visible sexually dimorphic characters (except for the structure of abdominal tip). In the case of *D. frenatalis*, it is more likely that the males are attracted to pheromone-releasing females on the underside of leaves at night, and remain there during the day. Further investigation of the mating behavior of each species will help clarify the behavioral factors underlying the formation of crambid adult assemblages.

The known localities of *D. frenatalis* are discontinuous: the Nicobar Islands, Sumatra, Hong Kong, and the Ryukyu Islands. Moreover, this species has not been rediscovered at its type locality, the Nicobar Islands, in recent years (B. Sumit Kumar Rao pers. comm.). In this study we found that *D. frenatalis* is abundant in mangrove environments. The scarcity of records for this species may reflect its specialized habitat. Further surveys of mangrove environments may lead to its rediscovery in known localities or discovery of new habitats in other regions. However, *D. frenatalis* was not detected in Murphy’s (1990) comprehensive survey of Singapore mangrove environments, which reported 102 herbivorous insect species attacking nine principal tree taxa. This suggests that *D. frenatalis* is likely absent from Singapore mangrove environments, and therefore it cannot be ruled out that the possibility that the distribution of this species is highly localized.

Acknowledgements

We are grateful to Dr Richard Mally (Czech University of Life Sciences Prague, Prague, Czechia) for providing the type specimen photographs and valuable information regarding its identification and tribal placement, and Dr David Lees (NHMUK) for granting permission to use the type specimen photographs. We also thank to Dr B. Sumit Kumar Rao (National Vector Borne Disease Control Programme, National Health Mission-State Health Society, Sri Vijaya Puram, Andaman and Nicobar Islands, India) for sharing on the recent occurrence

of *D. frenatalis* in the Nicobar Islands. Our appreciation extends to Dr Utsugi Jinbo (NSMT), the late Mr Masakatsu Kinjo, and Dr Shinichi Katada (Tokyo Kasei University, Japan) for allowing us to examine the specimens at NSMT and RUMF. We further thank to Mr Itsuzai Aoki (Okinawa Prefecture, Japan), Mr Fukashi Ishiwata (Kagoshima Prefecture, Japan), and Mr Takahiro Mano (Aichi Prefecture Japan) for kindly providing specimens. Additionally, we sincerely thank Dr Shen-Horn Yen (National Sun Yat-sen University, Taiwan), Dr Maria Alma Solis (Systematic Entomology Laboratory, Beltsville Agriculture Research Center, Agricultural Research Service, US), and Dr B. Sumit Kumar Rao for reviewing our manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was partially supported by the Collaborative Research of Tropical Biosphere Research Center, University of the Ryukyus (to YM), JSPS KAKENHI Grant Number 25K09163 (to NW) and University of the Ryukyus Research Project Promotion Grant for Young Researchers, No. 24SP04106 (to NW).

Author contributions

Conceptualization: YM. Data curation: YM, NW. Formal analysis: YM, NW. Funding acquisition: NW, YM. Investigation: YM, NW, YY. Methodology: YM, NW, YY. Project administration: YM. Resources: YM, NW, YY. Software: YM, NW. Supervision: YM, NW. Validation: YM, NW, YY. Visualization: YM. Writing – original draft: YM. Writing – review & editing: YM, NW, YY.

Author ORCIDs

Yuki Matsui  <https://orcid.org/0000-0002-0434-7111>

Nakatada Wachi  <https://orcid.org/0000-0001-9958-5093>

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

- Birch MC, Poppy GM, Baker TC (1990) Scents and eversible scent structures of male moths. *Annual Review of Entomology* 35(1): 25–54. <https://doi.org/10.1146/annurev.en.35.010190.000325>
- Downey JC, Allyn AC (1975) Wing-scale morphology and nomenclature. *Bulletin of the Allyn Museum* 31: 1–32.
- Hampson GF (1896) *The Fauna of British India, Including Ceylon and Burma. Moths.*—Vol. IV. Taylor and Francis, London, i–xxviii, 1–594.

- Inoue H (1982) Pyralidae. In: Inoue H, Sugi S, Kuroko H, Moriuti S, Kawabe A (Eds) Moths of Japan. Kodansha, Tokyo, Vol. 1: 307–404; Vol. 2: 223–254, pls 36–48.
- Inoue H, Yamanaka H (2006) Redescription of *Conogethes punctiferalis* (Guenée) and descriptions of two new closely allied species from Eastern Palaearctic and Oriental Regions (Pyralidae, Pyraustinae). *Tinea* 19(2): 80–91.
- Kimura T, Honda H (1999) Identification and possible functions of the hairpencil scent of the yellow peach moth, *Conogethes punctiferalis* (Guenée) (Lepidoptera: Pyralidae). *Applied Entomology and Zoology* 34(1): 147–153. <https://doi.org/10.1303/aez.34.147>
- Kimura T, Sakai J, Honda H (2002) Microstructure and pheromone producing function of male hairpencils in the yellow peach moth, *Conogethes punctiferalis* (Lepidoptera: Pyralidae). *Entomological Science* 5(2): 237–247.
- Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution* 33(7): 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Lederer J (1863) Beitrag zur Kenntnis der Pyralidinen. *Wiener Entomologische Monatschrift* 7: 243–280, 331–502.
- Maes KV (1985) A comparative study of the abdominal tympanal organs in Pyralidae (Lepidoptera) I. Description, terminology, preparation technique. *Nota Lepidopterologica* 8: 341–350.
- Mally R, Hayden JE, Neinhuis C, Jordal BH, Nuss M (2019) The phylogenetic systematics of Spilomelinae and Pyraustinae (Lepidoptera: Pyraloidea: Crambidae) inferred from DNA and morphology. *Arthropod Systematics & Phylogeny* 77: 141–204.
- Mandal DK, Bhattacharya DP (1979) On the Pyraustinae (Lepidoptera: Pyralidae) from the Andaman, Nicobar and Great Nicobar Islands, Indian Ocean. *Records of the Zoological Survey of India* 77(1–4): 293–342. <https://doi.org/10.26515/rzsi/v77/i1-4/1979/161857>
- Matsui Y, Mally R, Kohama S, Aoki I, Azuma M, Naka H (2022) Molecular phylogenetics and tribal classification of Japanese Pyraustinae and Spilomelinae (Lepidoptera: Crambidae). *Insect Systematics & Evolution* 54(1): 77–106. <https://doi.org/10.1163/1876312X-bja10037>
- Matsui Y, Hamaguchi J, Yagi S, Hirowatari T (2024) Two remarkable new species of *Glaucoccharis* (Lepidoptera, Crambidae, Crambinae) from the Ogasawara Islands, Japan. *Zootaxa* 5543(1): 83–96. <https://doi.org/10.11646/zootaxa.5543.1.4>
- Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R (2020) IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Molecular Biology and Evolution* 37(5): 1530–1534. <https://doi.org/10.1093/molbev/msaa015>
- Murphy DH (1990) The natural history of insect herbivory on mangrove trees in and near Singapore. *The Raffles Bulletin of Zoology* 38(2): 119–204.
- Nuss M, Landry B, Vegliante F, Tränkner A, Mally R, Hayden J, Segerer A, Li H, Schouten R, Solis MA, Trofimova T, De Prins J, Speidel W (2003–2025) Global Information System on Pyraloidea. <http://www.pyraloidea.org/> [Accessed 24 Jan 2025]
- Pajni HR, Rose HS (1977) Studies on the north-western species of *Dichocrocis* and *Lygropia* (Lepidoptera: Pyraustinae). *Oriental Insects* 11(4): 505–511. <https://doi.org/10.1080/00305316.1977.11090921>
- Robinson GS, Tuck KR, Shaffer M (1994) A Field Guide to the Smaller Moths of South-East Asia. Malaysian Nature Society, Kuala Lumpur, 309 pp.

- Solis MA, Phillips-Rodríguez E, Hallwachs W, Dapkey T, Janzen DH (2020) *Asturodes Amsel* (Lepidoptera: Crambidae: Spilomelinae): three new species from the Western Hemisphere and food plant records from Area de Conservación Guanacaste, Costa Rica. *Proceedings of the Entomological Society of Washington* 122(1): 147–171. <https://doi.org/10.4289/0013-8797.122.1.147>
- Speidel W, Mey W (1999) Catalogue of the Oriental Acentropinae (Lepidoptera, Crambidae). *Tijdschrift voor Entomologie* 142(1–2): 125–142. <https://doi.org/10.1163/22119434-99900025>
- Sutrisno H (2002) Cladistic analysis of the Australian *Glyphodes* Guenée and allied genera (Lepidoptera: Crambidae; Spilomelinae). *Entomological Science* 5(4): 457–467.
- Tomazovic G, Grootaert P (2010) Asilidae (Diptera) from mangrove, an unusual habitat for robber flies (Southeast Asia, Singapore). *Bulletin de la Société Royale Belge d'Entomologie* 146: 151–156.
- Utsugi N (2006) A new record of the genus *Maira* (Diptera: Asilidae) from Japan. *Hana Abu* 22: 70. [In Japanese]
- Walker F (1859) Part XIX. –Pyralides. List of the Specimens of Lepidopterous Insects in the Collection of the British Museum 19: 799–1036.
- Whitaker T, Sutton S, Barlow H (2023) A preliminary guide to pyraloid moths of Borneo. Part 2. Pyraloidea: Crambidae (1st part) *sensu* Regier JC et al. 2012. Natural History Publications (Borneo) Sdn. Bhd., Kota Kinabalu, Sabah, 82 pp.
- Yoshiyasu Y (1984) A study of Thailand Nymphulinae (Lepidoptera, Pyralidae) (3) Two new species of *Eristena* Warren. *Tyô to Ga* 35: 1–9.
- Yoshiyasu Y (2017) Various hosts and habits of pyraloid moths, with two crambid species feeding on seaweeds. *The Nature and Insects* 52: 5–9. [In Japanese]

Supplementary material 1

Forewing lengths (mm) of male and female *Dichocrocis frenatalis* specimens used in the statistical analysis

Authors: Yuki Matsui, Nakatada Wachi, Yutaka Yoshiyasu

Data type: xlsx

Explanation note: **table S1**: Forewing lengths (mm) of male and female *Dichocrocis frenatalis* specimens used in the statistical analysis. M = male; F = female. “#” indicates the sample number corresponding to Suppl. material 2: table S2. R script used for statistical analysis of forewing length data. A Welch’s t-test was conducted using R to compare the mean forewing length between male and female specimens.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.1243.155924.suppl1>

Supplementary material 2

Detailed information for *Dichocrocis frenatalis* specimens examined in this study

Authors: Yuki Matsui, Nakatada Wachi, Yutaka Yoshiyasu

Data type: xlsx

Explanation note: **table S2**: Detailed information for *Dichocrocis frenatalis* specimens examined in this study. Sample number (“#”), collection start and end days, month, year, total number of individuals (N Ind), number of males (N male), number of females (N female), locality island, detailed locality, preservation and preparation status of specimens (Specimen), collector (Collected by), associated species or ecological context (Associated), and additional notes (Note). Some sample numbers correspond to those shown in Suppl. material 1: table S1.

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zookeys.1243.155924.suppl2>